

THE VEGETATION OF THE BAY OF FUNDY SALT
AND DIKED MARSHES: AN ECOLOGICAL STUDY.

CONTRIBUTIONS TO THE ECOLOGICAL PLANT-GEOGRAPHY
OF THE PROVINCE OF NEW BRUNSWICK, NO. 3.

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(Continued from p. 302.)

Synopsis of the grouping of the vegetation of the marshland.

A. HALOPHYTIC DIVISION, including the halophytic formations
or HALOPHYTIA.

I. *Wild salt-marsh formation (Limnodium).*

1. *Spartina stricta* or *sedge* association, or SPARTINETUM.
2. *Salicornia-Suaeda* or *samphire* association, or SALICORNETUM.
3. *Statice-Spartina juncea* or *fox-grass (mezotte)* association, or
STATICETUM.

B. MESOPHYTIC DIVISION (Culture section), including the meso-
phytic formations or MESOPHYTIA.

II. *Reclaimed salt-marsh formation = meadow formation
(Poa).*

4. *Phleum-Agropyrum* or *timothy-couch* association, or PHLEUM-
ETUM.
5. *Roadside weed* association, or CNICETUM.

C. HYDROPHYTIC DIVISION, including the hydrophytic formations
or HYDROPHYTIA.

III. *Wet-marsh formation (Telmatium).*

6. *Spartina cynosuroides* or *broadleaf* association, or MACROSPAR-
TINETUM.
7. *Carex-Aspidium* or *bog-marsh* association, or ASPIDETUM.

IV. *Bog formations.*

8. *Carex-Menyanthes* or *floating bog* association, or CARICETUM.
9. *Heath* or *flat-bog* association, or ERICETUM.
10. *Sphagnum* or *raised bog* association, or SPHAGNETUM.

V. *Water margin formation (Nematium).*

VI. *Swamp formation (Helorgadium).*

A. HALOPHYTIC DIVISION (HALOPHYTIA).

Consists of herbaceous plants of compact low growth, small size, and xerophytic structure, these features being determined by the presence of much salt, which both prevents the ready absorption of water requisite for large size and diffuse habit, and also, being itself injurious to the vital processes and not removable by plants from the absorbed water, requires the development of water-conserving adaptations to prevent its concentration in the tissues by transpiration. The division here includes but a single formation.

I. THE WILD SALT-MARSH FORMATION (LIMNODIUM).

Consists of slender-rooted and surface-following grass-like plants (this feature being determined by the fineness and compactness, and hence the poor aeration of the soil, which does not permit thick roots), mostly wind- or self-pollinated and wind-disseminated and late blossoming. The area of the salt-marsh has been restricted to a small fraction of the original area by reclamation through diking, and includes at present only a fringe outside the dikes,³⁶ together with certain points (shown in *fig. 2*) unprofitable from their form to dike. The formation here includes three associations.

I. THE SPARTINA STRICTA, OR "SEdge" ASSOCIATION, OR SPARTINETUM.

The characteristic association of the immediate edge of the salt water extending typically as a belt just above and below ordinary high-tide mark and further distinguished to the eye by its bright green color, and the stiff habit and close growth of its plants (*figs. 7, 8, 9, 10, 11*). It extends also in isolated clumps much below high-water mark (the "sedge-bogs"), follows the ditches inside the dikes, occupies depressed areas amongst the Staticetum on high marsh, and takes possession of the lakes in process of reclamation. The association comprises but a single vegetation-form as follows:³⁷

³⁶ This fringe extends not only along the sea but also along the rivers to near their heads (as shown by *fig. 7*), though for the sake of clearness this is not shown on the map, *fig. 2*.

³⁷ There occurs sometimes with it, or at all events in its situation, and especially on the little "cliffs" where the high marsh is being worn away, an abundance of a green alga, *Enteromorpha clathrata* (Roth.) J. Ag. (auc. G. T. Moore).

SPARTINA STRICTA GLABRA Gray. *Spartina stricta maritima* (Walt.) Scribn. *Figs. 9-10.*—Called in the marsh country *sedge* (usually pronounced "sage"). The most characteristic and extreme

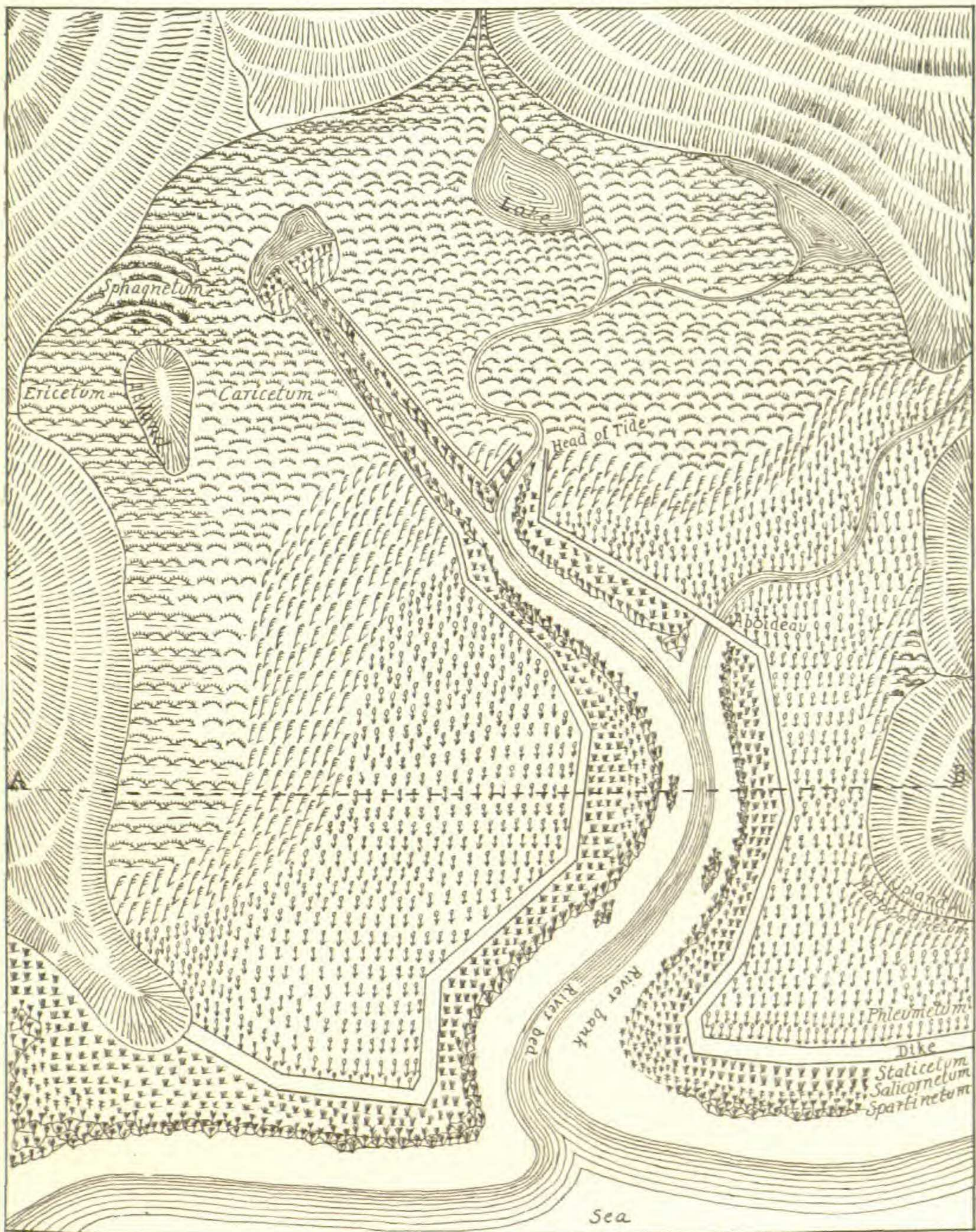


FIG. 7.—Diagrammatic map of a typical portion of the marshland, showing the ideal distribution of the principal associations (excepting the *Aspidetum*, on which see *infra*). In the upper left hand is a lake in process of reclamation; on the river banks are represented three of the "sedge-bogs." The line *AB* is the position of the cross-section shown in *fig. 8*.

salt-enduring plant (halophyte) of the marshes, following everywhere except on the newest marsh the margin of the salt water, from the open sea, where it is stunted to 6ⁱⁿ (15^{cm}) or less in height, along the tidal rivers, where it forms on their sloping banks much below high-tide mark dense clumps of a few square feet in area (locally called "sedge-bogs"), following the salt water through leaky sluices inside the dikes, and elsewhere in ditches behind the dikes, and reaching its perfection of size, some 3 to 4^{ft} (1 to 1.30^m) in the brackish water of the lakes in process of filling with new mud. It is the dominant and the only member of the association (*Spartinetum*) in which it occurs.

This species is a very typical representative of an important

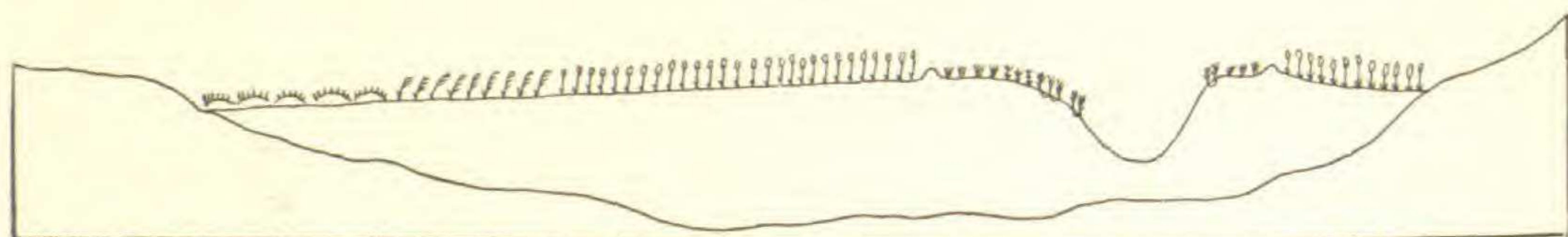


FIG. 8.—Cross-section of the region represented in *fig. 7*, at the dotted line.

vegetation-form. It consists of a system of perennial branching rootstocks running just beneath the surface, well sheathed by leaf bases, giving off extremely slender roots, protected by a fine-celled, thick epidermis and containing numerous large air passages, which, in connection with those of the leaves, explain the plant's power to withstand prolonged immersion. From the rootstocks rise frequent short vertical stems, completely and tightly enwrapped and protected by the bases of the half dozen or more stiffly erect, more or less inrolled slender leaves, their sizes varying inversely with the degree of salt to which they are exposed. The leaves are smooth on the back, which is covered by a very small-celled, thickly cutinized epidermis supported by a collenchymatous and sclerenchymatous hypodermis, and is probably quite impenetrable to water and gases; their inner face, however, is folded into deep grooves, at the bottoms of which lie few stomata, with the large water-storing cells near them. The mechanism appears to be such that the fulness of the latter cells holds the leaf flat, thus opening the grooves, giving the stomata free outlet to the atmosphere outside, but the withdrawal of

some of this water allows the elastic back to curl the leaf and close up more or less the grooves and hence protect the stomata, one of the most efficient regulatory mechanisms to control transpiration according to water supply known to me. Chlorenchyma is palisaded especially towards the inner face; large air spaces exist, communicating with those of the root, and the epidermis is not wetted by water, all permitting the immersion of the plants



FIG. 9.—Showing the three typical associations of the salt marsh. The *Spartinetum* on the left and the *Staticetum* (with its marginal *Statice*) on the right are advancing upon the *Salicornetum* in the center.

for some time. It propagates apparently mostly by root-stocks, and good seeds and seedlings appear to be rare. It is wind-pollinated and wind-disseminated.

Its specific physiological correlations appear to be unstudied. On account of the failure of all my seeds to germinate, I was unable to determine the resistance of its root-hairs to plasmolysis, but analogy with *Salicornia* would lead us to expect a high degree of resistance.³⁸

³⁸ It seemed to me likely that the power of the halophytes to stand salt might be connected with a power in their root-hairs to withstand plasmolysis by sea water. Accordingly I procured some pure sea-water from Baie Verte, N. B., and, with distilled

The ability of this form to occupy its peculiarly trying habitat, with its abundant salt, frequent and prolonged immersion, and shifting substratum are amply explained by its adaptive structures above considered, notably its xerophytic anatomy combined with a very perfect transpiration-regulating mechanism, its capacity for copious air storage, and its system of interlacing, firmly anchored rootstocks, to which may be added the probable specific power of its root-hairs to resist plasmolysis by salt water. It is of course because no other plant possesses anywhere near the same combination of qualities that it reigns supreme, without competitor or companion, in its own peculiar habitat. There are forms which can stand as much immersion, and forms which can stand as much salt, but no forms which can stand a combination of these two conditions in so extreme a degree.

Like all other associations it tends to spread outside its own typical habitat. With the slow, irresistible, phalanx-like advance of its rootstocks, it easily enters the habitat of the *Salicornetum*, and utterly defeats and destroys that association; it then advances upon the *Staticetum* against the margin of which it can prevail, to some extent, but ultimately it is overcome by that association, excepting where depressions with their salter soil enable colonies of it to thrive. In the lakes it is finally overcome by the broadleaf.

water, made solutions of all strengths from 10% to 90%. I gathered all the seeds of halophytes I could procure myself or by aid of a correspondent at Sackville (Mr. F. A. Dixon), and started them with fresh water in Zurich germinators. As soon as root-hairs appeared I tested them with the various solutions, and noted for each kind the solution which just initiated plasmolysis. I found a close correspondence between the halophilism of the plant and the power of its root-hairs to resist plasmolysis, the details being given with the various species in the following pages. This shows that the power of the plants to resist the salt water is correlated with and probably dependent upon the ability of the root-hairs to resist plasmolysis. This power has of course been gradually acquired, but what its physical basis is I do not know; though we shall probably find that substances osmotically equivalent to the salt of the sea-water have been formed in the sap of the hairs. In several cases (*Hordeum*, *Couch*) it was noticeable that no plasmolysis occurred with certain solutions as long as the hairs were alive, but it occurred after they were dead. Several forms (*Statice*, *Plantago*) showed marked jelly-like caps to the young roots, seemingly an adaptation to slower water-entrance. The study of the roots of these halophytes will give interesting results.

2. THE SALICORNIA-SUAEDA OR SAMPHIRE (LOCALLY CROWFOOT) ASSOCIATION, OR SALICORNETUM.

The characteristic association of the newly formed and forming marsh, occurring typically from the lowest high-tide marks to the highest marsh, hence overlapping the territory later occupied by the *Spartinetum* from below and the *Staticetum* from above, and further distinguished by its usually loosely open

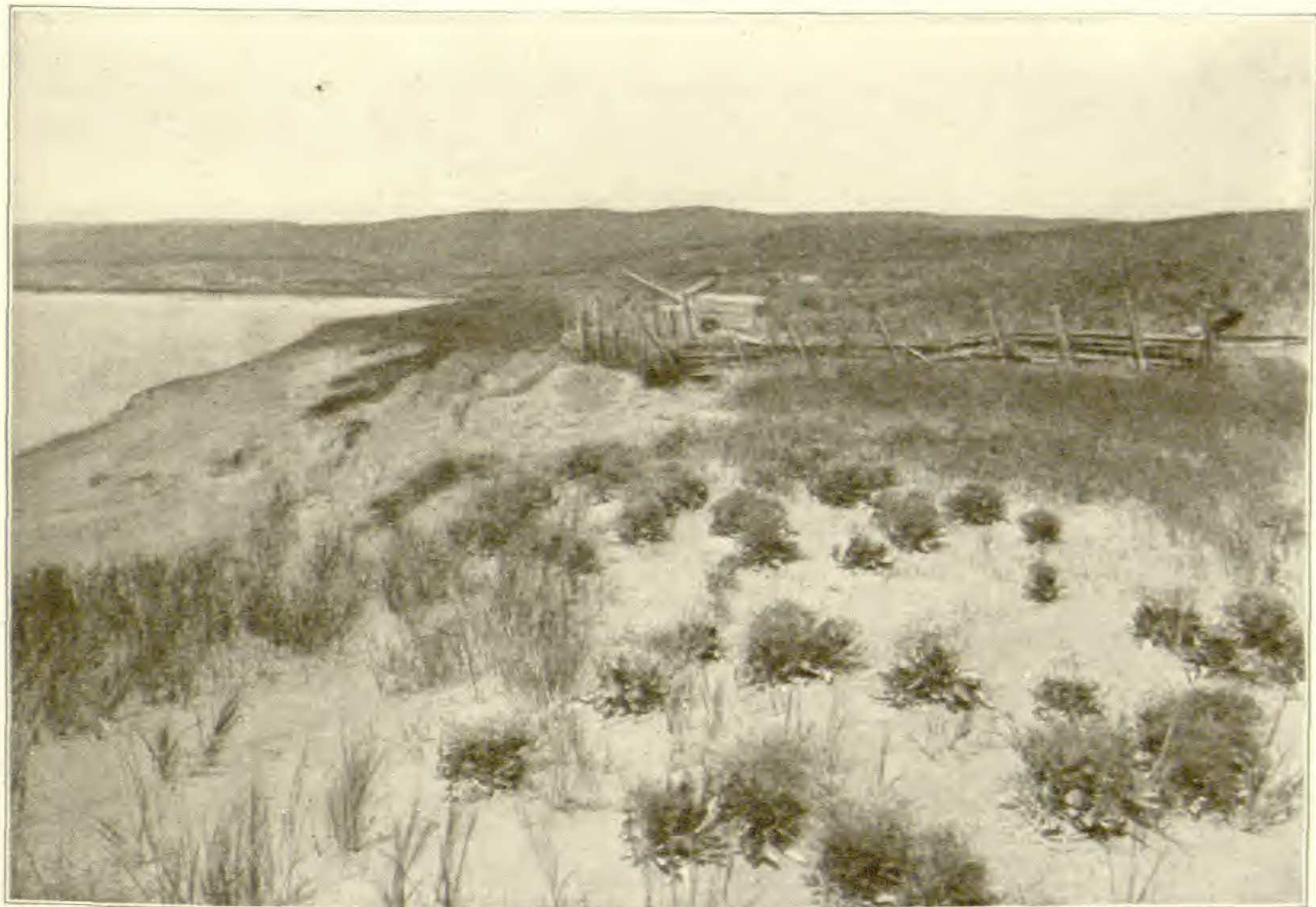


FIG. 10.—Showing *Spartinetum* on the left (and occupying a depression on the right) advancing upon the *Staticetum* (showing *Statice* clearly) in the center. *Salicornetum* obliterated between them as an association, but occurring as scattered individuals in the other associations. The fence-like structure is a protection to the dikes against the wash of the sea.

formation, the small size and succulent habit of its members, and their usually reddish color (*figs. 7, 8, 9, 12*). It extends inside the dikes, especially on newly flooded marsh, along the marsh roads and on the bald places, and upon any newly exposed marsh soil, as on new dikes, ditch margins, dredge-mud, etc. It is especially well developed where cattle run on the salt marsh, apparently because the cattle keep down the *Spartinetum* and *Staticetum*. In general its members are smaller, more stiffly upright, sparser, and redder the salter the place, and are more

luxuriant, larger, more spreading, and greener the fresher the place.

The association is composed of two dominant members, *Salicornia herbacea*, or samphire, and *Suaeda linearis*, which appear to be as a rule about equally abundant and prominent, and of two secondary forms, especially coming in on the higher and drier side, *Spergularia borealis* and *Atriplex hastatum patulum*.

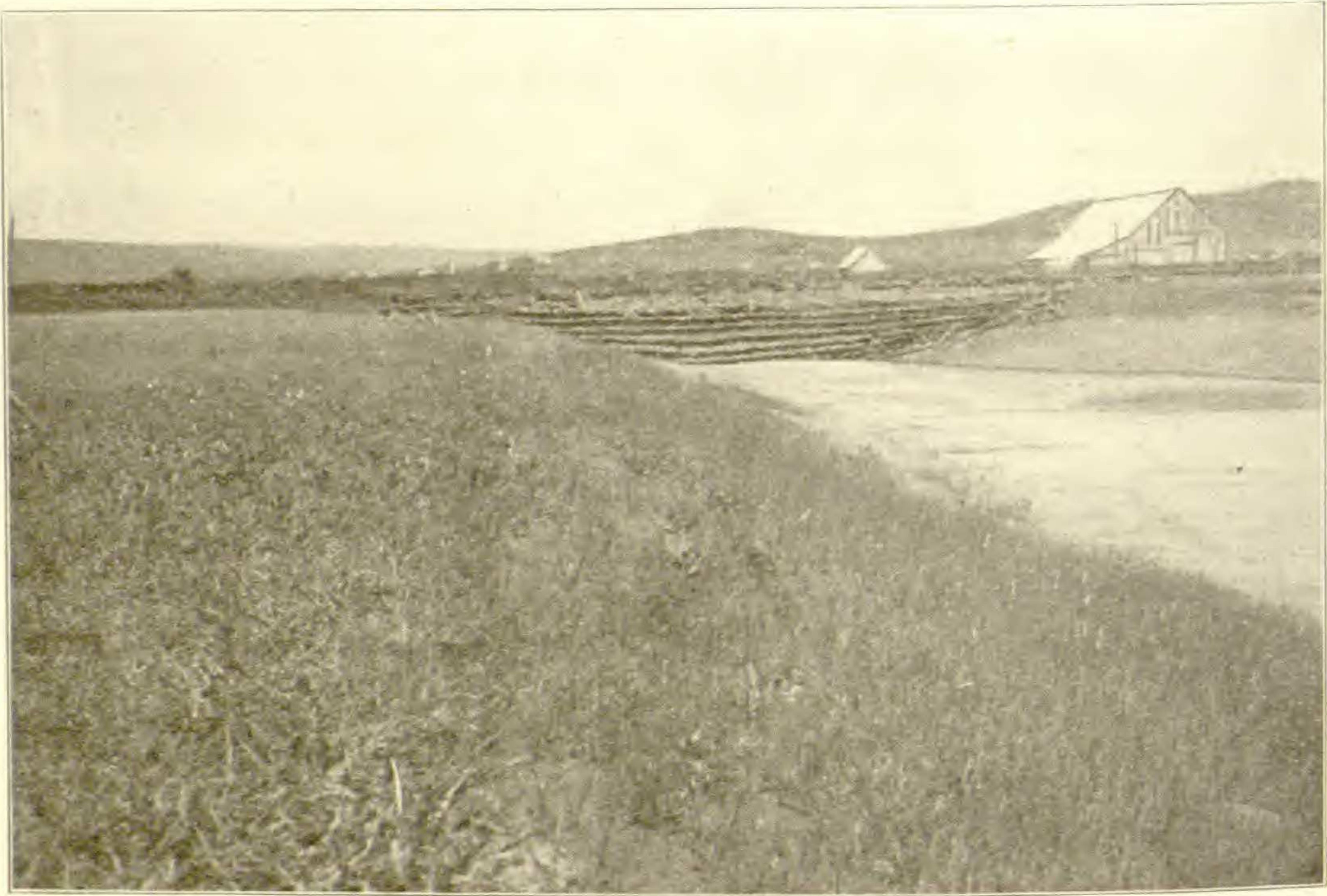


FIG. 11.—Showing Spartinetum on the river bank on the right advancing on the Staticetum on the left, with contact line in the center. The Statice can be seen within the margin of the Spartinetum. In the background is an aboideau crossed by a railroad.

SALICORNIA HERBACEA L.—Called in the marsh country crow-foot, and sometimes samphire. Next to the *Spartina* the most abundant and characteristic halophyte of the marshes, mixing occasionally with the *Spartina*, but commonly in a belt landward of it and hence in less wet situations; especially characteristic of the zone between the high-tide marks of neap and spring tides, and of newly forming marsh on convex river curves, where it is often the only plant for considerable areas, but being an annual it is somewhat irregular in distribution (*figs. 9-12*). In the saltiest

places it is not over three inches (8^{cm}) in height, red in color, and stiffly erect; extends also inside the dikes on the bald places and along the roads, where it may become several times larger, decumbent and spreading and clear green. The dominant member of the *Salicornetum*.

Its vegetation-form is well-known and characteristic. It is a fibrous rooted annual, with a jointed, branching, succulent, prac-

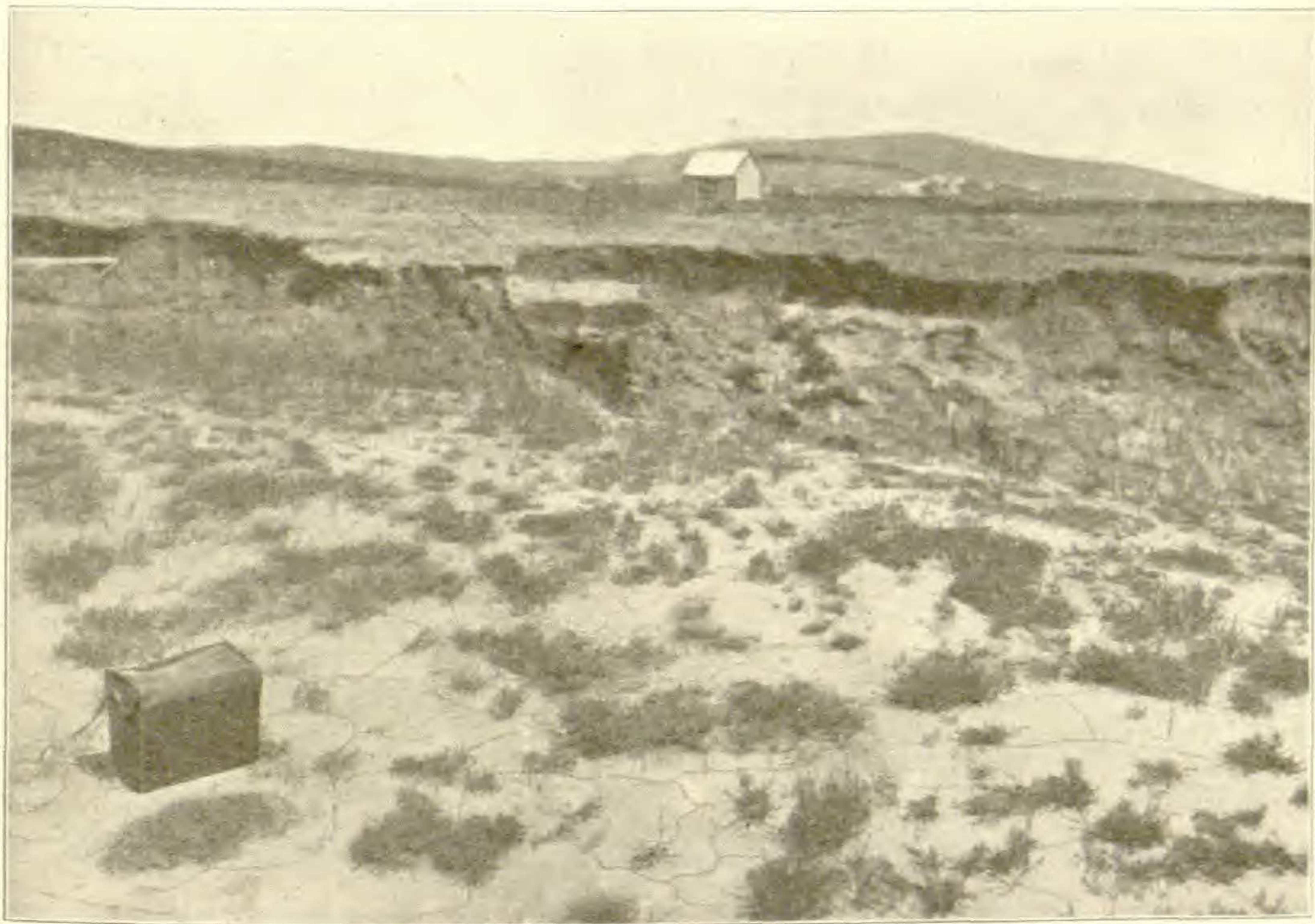


FIG. 12.—Showing a typical piece of *Salicornetum* on new marsh.

tically leafless stem, tending to verticality of green tissues, varying in size inversely with the saltness of the habitat. Its anatomy is markedly xerophytic, for in addition to the reduction of surface, the jointing and verticality described above, it possesses a compact stele (with cortical system of bundles replacing those of the abandoned leaves) thick water-storing cortex, dense palisaded chlorenchyma, small-celled thick-cuticled epidermis, small and narrow-slitted stomata, all markedly xerophytic features. The air storage system, however, is limited, consisting of intercellular spaces of ordinary size, and certain air-storing tracheids near the stomata. This is sufficient, however, to per-

mit the occasional immersion which the plant undergoes at the higher tides, but is insufficient to permit immersion so prolonged as that of *Spartina*. It is this feature that determines the difference in position of the two plants; the *Salicornia* can apparently stand as much salt as the *Spartina*, but it cannot stand long immersion, and hence it is confined to a higher position on the river banks.³⁹

The physiological correlations of the species appear not to have been studied. I have, however, found that the root-hairs of the seedlings can withstand without plasmolysis a solution of 90 per cent. pure sea-water, which fact helps to explain its halophytic capacity. It is wind-pollinated, and apparently, wind-disseminated, though the seeds are provided with hooked hairs. It appears to me to be polyembryonic.

SUAEDA MARITIMA Dumort. *Dondia maritima* (L.) Druce.— Appears to have no local name. Occurs most commonly intermixed with the *Salicornia*, though extending into less salt places, and forming the second member of the *Salicornetum* (*fig. 12*).

Vegetation-form in a general way approaching that of *Salicornia*, but a leaf- instead of a stem-succulent and much less markedly xerophytic. Its root-hairs can endure 60–70 per cent. salt water without plasmolysis. Fibrous-rooted annual with semi-succulent stem, usually prostrate but sometimes in saltless places erect, with efficient epidermis having a thick cuticle and much collenchyma, bearing numerous somewhat succulent bluish green slender leaves which can be up to 2ⁱⁿ (5^{cm}) long. Leaves with large rounded epidermal cells, and stomata about equal on all faces, dense palisaded chlorenchyma and some water-storing cells. The leaves afford some protection against transpiration to one another and the stem by overlapping. Little trace of air-storing system, and hence not enduring immersion well, which explains why it grows rather higher on the beaches than the *Salicornia*. It is wind-pollinated and apparently wind-disseminated.

SPERGULARIA BOREALIS Robinson. *Tissa Canadensis* (Pers.)

³⁹ Diehl's conclusions that this plant has a power of removing salt chemically from its tissues are not substantiated.

Britton.—Apparently has no local name in the marsh country. Occurs to some extent with the Suaeda and Salicornia but belonging to less salt and wet places than either, and hence characteristic of the very highest and driest spots of the wild marsh; especially prone to wander inside the dikes on low places and along the roads.

Vegetation-form nearly identical with that of Suaeda, but smaller, more profusely branched and decumbent, and more leafy, with the leaves somewhat more slender. It is of a brighter green than the preceding, and unlike any of the preceding, bears pale pink or whitish star-like apparently entomophilous flowers.

ATRIPLEX PATULUM L., vars. *hastatum* Gray and *littorale* Gray. *Atriplex patula* L. and *A. hastata* L.—Appears to have no recognized local name. Occurs with the Salicornia and Suaeda, especially on their drier side, when it is not much taller than they, as a rather inconspicuous member of the Salicornetum, but extends also upon the dikes, when it occurs as a band, usually on the inner, lower side of the dikes; extends also within the dikes, especially upon newly flooded marsh, where it may become waist high.

The species represents a distinct vegetation form, a fibrous-rooted annual with erect stem and petioled hastate (var. *hastatum*) or linear (var. *littorale*) leaves, the whole plant varying in size from a few inches on the saltiest places to near 3^{ft} (1^m) on newly flooded marsh. The plant exhibits in its vertically adjustable leaves which are extremely well marked in the young state on the salt marsh, in its thick cuticle, dense palisade, and its abundant covering of scales (giving it its characteristic scurfy or mealy appearance), xerophytic adaptations, adapting it to its halophytic habit. Its root-hairs endure nearly 40 per cent. salt water without plasmolysis. There appears to be no constant relation between the distribution of the linear and the hastate leaved forms and the environment, though each kind occurs as a rule largely by itself. It is wind-pollinated and wind-disseminated.

The chief characteristics of this association as a whole, its rapidity of appearance on new marsh and its ability to endure

much salt but little immersion, are amply explained by the adaptations of the members above described, notably their annual character and excellent mode of dissemination, their xerophytic structure, and the power of salt resistance possessed by their roots (at least in the two dominant members).

The members of the association grow often fairly intermingled, but elsewhere one or the other form may predominate, even for a considerable area, to the exclusion of the others. This irregularity of commingling is probably due to the fact that, all of them being annuals, the precise place of their occurrence in any given year is largely a matter of accident, due to the way the seed distributing agencies of wind and water happened to drift them the preceding year. Another irregularity comes from the general tendency for the *Salicornia* to be nearest the water, the *Suaeda* next, the *Spergularia* and *Atriplex* last, a distribution amply explained by the comparative degrees of xerophilism and air-storing capacity of the members, as above described.

Since the members are all annuals, all of nearly the same size, and all grow in an open order interfering little with one another, it is possible that this association is simply a mixture of forms which happen to be adapted to a similar habitat, with no ecological bond, but only coincident interests, between the members. Indeed, in the present state of knowledge, it is impossible to say that this is not the case with the members of all associations, though I think not, as will later be discussed.

Although thus very prompt to take possession of new marsh, this association can hold its ground only temporarily, for the slow-moving *Spartinetum* advances upon it from below, and the *Staticetum* upon it from above, until between the two it vanishes, and disappears as an association from old marsh, existing only as scattered individuals, visitors, among the other associations. It represents a sort of annual light infantry quick to occupy new territory, but easily displaced by the resistless advance of the heavy phalanxes of the perennial associations.

The readiness with which this association takes possession of new marsh makes it the first to appear on the new surface produced by artificial flooding. When the tide is shut out all the

members increase immensely in size, even, in the case of *Atriplex*, to waist high, after which they are displaced by the perennials. But this subject will be considered later under another heading.

3. THE STATICE-SPARTINA JUNCEA, OR FOX-GRASS (LOCALLY MEZOTTE) ASSOCIATION, OR STATICETUM.⁴⁰

The characteristic association of the highest salt marsh, overflowed only by exceptionally high tides, and representing the highest development of salt-marsh vegetation—its matured condition (*figs. 7, 8, 9, 10, 11, 13, 14*). Distributed on all the



FIG. 13.— Typical piece of mature Staticetum showing *Hordeum* (barley-grass,) prominent in the center, and some scattered *Spartina cynosuroides* (broadleaf), etc. The finer grass is the *Spartina juncea* (fox-grass), and with it is some Statice.

highest parts of the wild salt marsh, and occupying the berme-bank built by the sea along the rivers outside of the dikes, and distinguished by its dull-green color in various shades, and the very dense, almost turf-like growth of its grass-like plants. It forms real salt meadow (yielding the salt-marsh hay), but is little luxuriant as compared with the meadows of the reclaimed marsh. It does not often, if at all, extend as a whole within the dikes, although some of its members do. Its dense growth appears to enable it to stop some of the mud brought to it by the very high-

⁴⁰ Statice is not so characteristic of this formation as is *Spartina juncea*, and it would be better called *Spartinetum* were that name not preempted for the *Spartina stricta* association, which latter having but a single member, of course admits of no other name.

est tides, by which, with the aid of its own decaying parts, it can build itself somewhat above the marsh, thus affording conditions for a limited mesophytic herbaceous vegetation, though this appears never to go very far, and never to include any woody plants whatsoever. In other places, small abrupt knolls of similar vegetation occur, which appear to be due to low hillocks pushed up by floating ice, though this point is uncertain. This association is composed of two dominant, with several secondary and some occasional members, as follows:

STATICE LIMONIUM CAROLINIANUM Gray. *Limonium Carolinianum* (Walt.) Britton.—Locally called wild cabbage. A very characteristic plant of the marshes, an important member of the dense vegetation of the high marsh with which it is much intermixed, and beyond which it extends in scattered clumps on new marsh, thus forming the vanguard in the advance downward upon the Salicornetum; also frequently in a band along the lower outer side of the dikes (*figs. 10, 11*).

A very marked vegetation-form, and the only one of the kind on the marsh; a rosette perennial, producing a cluster of radical petioled broad smooth leaves, usually so numerous as to afford one another much protection, and capable of much change of position according to surroundings. The plants are smallest on the saltiest places, with leaves but 2-3ⁱⁿ (5-8^{cm}) long, and largest on the high grassy marsh when the leaves may be nearly 12ⁱⁿ (30^{cm}) long. Its leaves, stem, and root all possess a very abundant mucilage (apparently its chief xerophytic character), occurring even in the epidermis, and apparently intermixed with much tannin (which turns the plant black in formalin), a well but not extremely developed epidermis and cork. Its root-hairs can endure 50 to 60 per cent. of salt water without plasmolysis. It appears to attain its full size in a single season from seed, which explains the rapidity with which it takes possession of new marsh. It blossoms very late (in full bloom August 27, 1899), like other halophytes. Insect- and wind-pollinated. Like some other halophytes, it forms a jelly coating around its young roots, especially at the cap.

PLANTAGO MARITIMA L.—Locally called goose tongue. Occurs

abundantly among the *Statice*, especially as the latter advances on new marsh and at times in areas by itself; also sparingly with the *Spartina juncea*, as a fairly constant but not prominent member of the *Staticetum*.

A distinct vegetation-form, a stemless perennial with radical cluster of a few succulent linear leaves, giving it a somewhat grass-like habit. Its structure is moderately xerophytic, with thick cuticle and densely palisaded chlorenchyma. Wind-pollinated and wind-disseminated. Its size varies from 3 or 4ⁱⁿ (7-10^{cm}) high in the saltiest places to 12ⁱⁿ (30^{cm}) in less salt places. It forms a jelly coating over its root cap, and can withstand nearly 60 per cent. of salt water without plasmolysis.

SPARTINA JUNCEA Willd. *Spartina patens* (Ait.) Muhl.—Fox grass or mezotte.⁴¹ The most abundant and characteristic grass of the high salt marsh, intermingled with the other plants in the *Staticetum*, and also occurring in dense mats, especially in the slight depressions next the dikes. Rarely cut for hay. (*Figs. 13, 14.*)

A representative vegetation grass-form, composed of slender branching rootstocks, sending down very slender roots, and sending up very copious culms 6-12ⁱⁿ (15-30^{cm}) in height, bearing slender inrolled leaves of somewhat xerophytic structure.

PUCCINELLIA MARITIMA Parl.—Occurs amongst the *Statice* in isolated bunches, and also in larger isolated patches amongst the *Spartina juncea*. Distinguished from the *Spartina* by its larger size, lighter color, and tendency to grow in radiating tufts.

A vegetation-form not very different from the *Spartina juncea* but tending to grow somewhat after the manner of a bunch grass, especially as it appears on new marsh.

FESTUCA OVINA L.⁴²—Occurs intermingled with *Spartina juncea* and *Puccinellia*, and very like them in vegetation type.

JUNCUS GERARDI Loisel.—Black grass. Occurs in dense radi-

⁴¹ So pronounced locally; it is an Acadian French word, used (as *misette*) in 1685 or earlier (Casgrain, *Un pèlerinage au pays d'Évangéline*—29. Paris, 1890.).

⁴² When the *Puccinellia* and *Festuca* grow together densely, as they sometimes do on the marsh, it is not easy to distinguish them unless in blossom, and I may be somewhat in error as to their relative abundance and part in the association. It is possible, too, that some others may occur which for this reason I have missed.

ating clumps in the Staticetum, but not especially abundant. Vegetation-form approaching closely to the grasses amongst which it grows.

TRIGLOCHIN MARITIMA L.—Scattered irregularly and not abundantly in the Staticetum, but more abundantly on the wet fresh marsh. Vegetation-form closely approaching the grasses amongst which it grows.

HORDEUM JUBATUM L.—Barley grass. Occurs upon the highest

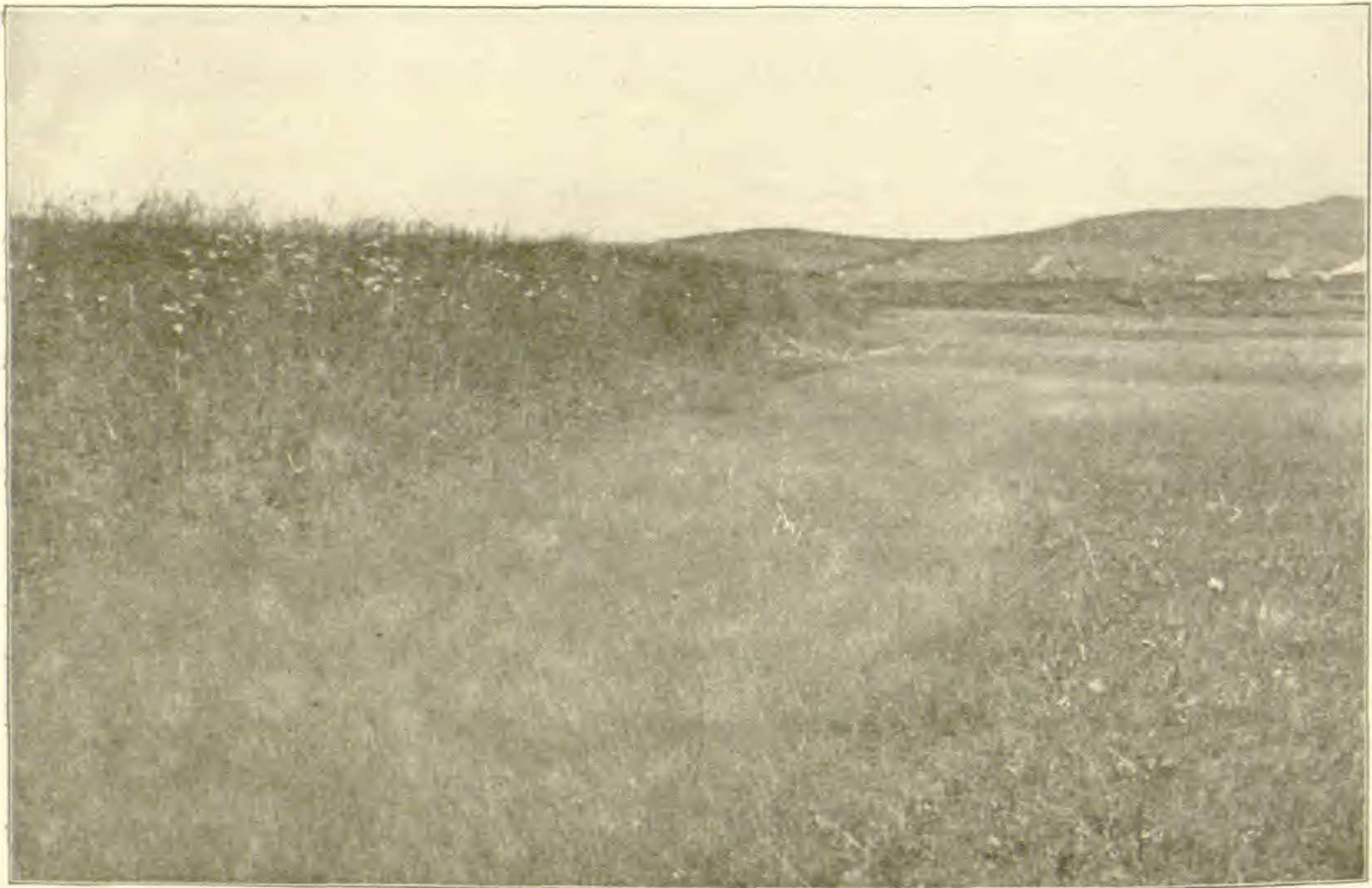


FIG. 14.—Showing a dike with *Agropyrum* (Couch) on the left, and typical Staticetum on the right. Beside the dike, in the center, is a zone of pure *Spartina juncea* (fox-grass).

part of the salt marsh (*fig. 13*), where it often is in great abundance and very conspicuous; also on the dikes in places, and especially abundant upon newly flooded marsh.

Vegetation-form near to other grasses, but with an unusually perfect system of dissemination, and apparently able to grow as an annual, whence the rapidity with which it enters new places. Its root-hairs stand over 40 per cent. pure salt water without plasmolysis.

GLAUX MARITIMA L.—Occurs scattered among the other members of the Staticetum, and apparently little gregarious.

A perennial herb of somewhat fleshy structure, not occurring in as salt places as its appearance would imply.

All of the members of this association are characterized by a moderately xerophytic structure, but with little provision for air storage, explaining well their position as occupants of the high marsh, which is rarely overflowed and from which a part of the salt at least is removed by superficial drainage.

The dominant members of the association are the *Spartina* (fox-grass or mezotte) and the *Statice*, with the *Puccinellia* and *Plantago* as important secondary members, and *Festuca*, *Juncus*, *Triglochin*, and *Hordeum* as less important, while *Glaux* is subordinate. The *Spartina* is the most important of all, forming the greater part of the association on the high marsh, and occurring here and there, especially in the slight depressions just outside the dikes (*fig. 14*), in large stretches unmixed with the others. In such places it forms a dense close turf. Elsewhere the *Statice* occurs intermingled with it (*figs. 9, 13, 14*), probably in such positions deriving some protection from transpiration for its broad leaves by the shade of the *Spartina*, but the *Statice* is especially important as the marginal member of the association particularly in its advance upon new marsh (*figs. 9, 10, 11*). It advances upon and displaces the *Salicornetum*, and then engages the *Spartinetum* advancing up the beach, the two associations mingling along the line to some extent (*figs. 10, 11*). The line of contact between these two represents one of the lines of competition to which I have given much study, with no results of value. When advancing in this way upon new marsh the *Statice* often forms so distinct a band that one is tempted to assign it to an association by itself, the more especially as it also so often occurs in a band on the angle of the dikes just inside of the fox-grass (*fig. 15*); but the luxuriance with which it grows along with the fox-grass shows it to be properly a member of the same association with that, while its distinctness on new marsh is plainly due simply to its more rapid power of spread. Closely following and intermingling with the *Statice* comes the *Plantago*, which also sometimes exhibits an indistinct band by itself, particularly between fox-grass and *Statice*. Intermingled with the

fox-grass comes the *Puccinellia*, which occurs in scattered dense radiating clumps, like a bunch-grass, in part here and there amongst the fox-grass, from which it is distinguished by its lighter color, and in part as scattered clumps on new marsh following the *Statice* in its advance. The *Festuca* is less common but grows somewhat after the same manner, as indeed does the *Juncus* or black grass. *Triglochin* occurs scattered among the other members, and seems equally at home here and in the fresh-water associations later to be noted, and *Glaux* is likewise scattered. *Hordeum* comes in only when the association reaches its greatest development on the highest marsh, and it occurs often as a band on the dikes above the other members. Scattered plants of *Spartina stricta*, *Salicornia*, *Suaeda* and *Atriplex* also occur as visitors, especially with the *Statice*. When this association reaches its greatest development on the highest marsh, it consists of a dense closed growth of all of the forms intermingled, and this constitutes the characteristic mature marsh. Upon it then develops the *Hordeum* (*fig. 13*). In this condition it can apparently build itself somewhat above the general marsh level, in part through the aid of the mud held by the plants when brought to them by the occasional extreme tides, and in part from the decay of their own members; and upon the higher places of this kind come in the occasional visitors, the broadleaf (*Spartina cynosuroides*), the couch (*Agropyrum vulgare*), *Potentilla anserina*, goldenrods, and others. But these represent the highest development; so far as any parts of the marshes now show, no woody vegetation ever gains a foothold.

It is plain that within this association while the members occur variously intermingled, there is some differentiation of position. Thus, typically the marginal member is the *Statice*, which is followed by the *Plantago* and the *Puccinellia*, while the fox-grass comes next, then the *Festuca*, *Juncus*, *Triglochin*, *Glaux*, and finally the *Hordeum*. Further, the marginal members tend to some extent to lessen, or even disappear towards the central or higher parts. This tendency to a zonal arrangement shows itself with great clearness upon the outer faces of the dikes, where there is usually a band of *Statice* at the lower angle,

then above it comes often a band of the *Hordeum*, above which comes the couch, later to be noticed.

The true ecological relationships of the several forms to one another, to what extent they are brought together simply by coincident habitat, to what extent they are of mutual benefit or disadvantage, to what extent some profit by the presence of others and those others are indifferent to them, to what extent and by what method they compete with one another, is unknown, and must be determined by the studies of the future. Such hints as we have upon these matters are little better than guesses, and such they will remain until thorough experimental study shall give the answer to these most difficult problems.

The interrelations of the three associations within the salt marsh formation have been sufficiently indicated in the preceding pages. In summary, the *Spartinetum* is the association of the extreme position where higher plant life is possible; the *Salicornetum* is the temporary association of new marsh; the *Staticetum* is the permanent association of the salt marsh in its highest natural state of development. On old marsh, the *Spartinetum* and *Staticetum* come together, obliterating the *Salicornetum*. The adaptations determining this distribution are known to us in a general way, but in details hardly at all.

(To be concluded.)